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RESPIRATORY ADAPTATIONS OF TWO BURROWING CRUSTACEANS, *CALLIANASSA CALIFORNIENSIS* AND *UPOGEBIA PUGETTENSIS* (DECAPODA, THALASSINIDEA) [1]

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Patterns of metabolic regulation among Crustacea range from metabolic dependence upon external oxygen tension to metabolic independence (Prosser and Brown, 1961; Wolvekamp and Waterman, 1960). Patterns of regulation are generally related to the ecology of the species concerned but only rarely are direct correlations made with the availability of oxygen in the habitat.

Thalassinid mud shrimps have a long evolutionary history as burrowers in marine sediments (Borradaile, 1903). It is well substantiated that mudflats are primarily hypoxic environments and presumably oxygen availability is a limiting factor to mudflat inhabitants (Brafield, 1964; Krogh, 1941; Pearse, Humm and Wharton, 1942). It may be expected that success in these habitats is in part predicated upon metabolic adaptation.

Very few published accounts of thalassinid respiration exist (Montuori, 1913). The purpose of the present investigation was to determine the effect of oxygen tension on the metabolic rate of two shrimps, *Callianassa californiensis* Dana and *Upogebia pugettensis* (Dana). Tolerance of anoxia was studied and preliminary measurements of post-anoxic respiration were made. This report attempts to relate ecological observations to the respiratory physiology of each species.

Materials and Methods

This study was conducted at the Oregon State University Marine Science Laboratory, Newport, Oregon, from April through June, 1966. Shrimps were collected at low tides from the exposed mudflats of Yaquina Bay. Specimens of *Upogebia pugettensis* were dug near Coquille Point on the north shore of the bay. A "shrimp gun," a cylindrical suction device similar to a "yabby pump" (Hailstone and Stephenson, 1961) was used to obtain *Callianassa californiensis* from the south shore of the bay near the marine laboratory.

Immediately after collection the shrimp were taken to the laboratory. The number collected, size, sex, and reproductive state were recorded at this time. The stages of the molt cycle could not be accurately determined; however postmolt individuals could be singled out by their light color, white setae, and softness of

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exoskeleton. All shrimp were maintained in containers previously filled with sand or mud obtained from the respective collecting areas, and were provided with flowing sea water (SW). The unfiltered SW contained sufficient organic detritus to maintain a number of animals in apparently good condition for as long as three months, as judged by full hind-guts and the formation of faecal pellets. No attempts were made to starve the animals. None of the animals used for experimental purposes was ever under laboratory conditions for more than two weeks.

The salinity of the laboratory SW ranged from 25.6‰ to 34.6‰ during the study period. The temperature range in the laboratory tanks during April–May was from 9°–13° C, but was slightly higher in June (10°–15° C).

Metabolic rate-oxygen tension measurements

An oxygen macro-electrode was used in conjunction with a Beckman Physiological Gas Analyzer (model 160) to determine the oxygen tension of SW under laboratory conditions. The oxygen electrode and the analyzer were calibrated before each experiment. Calibration solutions were made with SW whose salinity was identical to that used throughout each experiment. Since electrode performance varies widely with temperature, calibration was made at the temperature at which the sample measurements were to be made. All experiments and calibrations were carried out in a water bath at 10° C ± 0.2° C.

A zero oxygen calibration solution was obtained by using "Oxsorbent" (Burrell Corp.). Compressed air was used to obtain a fully air-saturated calibration solution. A value of 20.95% was used to express the concentration of oxygen in air. Empirical calibration of the gas analyzer meter was necessary to yield an absolute scale. Hence, SW samples representing different saturations were analyzed for oxygen content by a modified micro-Winkler method. In this fashion oxygen tension (mm Hg) was found to be directly proportional to oxygen concentration (ml/l) over the full range from zero to 100% air-saturation.

The following conditions were observed in all experiments. Only adult male shrimp, ranging from 3.4–8.7 g and in apparently good condition, were used. Animals were removed directly from the sand or mud substrate in the laboratory and placed in either a 0.2-liter or 0.4-liter jar, depending on the size of the shrimp, for one to two hours before the beginning of an experiment. During this period of adjustment the SW was kept at or near full air-saturation by aeration. The salinity of the water ranged from 31–35‰.

Within the jar the animal rested on a plastic screen supported above a magnetic stirring bar by a lucite cylinder. A water-driven underwater stirrer prevented stratification of oxygen within the jar. The performance of the oxygen electrode was empirically determined to be independent of the stirring rate. Rates as low as possible were used to minimize disturbance to the animal. Although activity of individuals was not monitored, animals were for the most part quiescent during determinations.

At the beginning of an experiment the jar was sealed with a rubber stopper through which the previously calibrated electrode and a breeder line had been inserted. As the shrimp depleted the oxygen the drop in oxygen tension was recorded from the analyzer at 15-minute or one-half-hour intervals. To arrive at an accurate measure of the volume of the jar, the volume of the animals was determined by

water displacement. Wet weights of the shrimp were taken on a Mettler balance at the completion of the run. All experiments were started around noon, lasting until the individual shrimp had lowered the oxygen tension to zero, *ca.* 12–24 hours. Using the micro-Winkler calibration values and the jar volume, the resulting time-tension curves were then translated into oxygen consumed per given time interval; final calculation resulted in ml O_2 consumed $\times$ gm wet body weight^{-1} $\times$ hr^{-1}. For comparative purposes 100% air-saturated SW at 10° C is equivalent to an oxygen tension of 160 mm Hg or a concentration of 6 ml O_2/l.

Heart rate measurements

The effect of slowly decreasing oxygen tension on the heart rate of *C. californiensis* was measured. The heart is covered by a relatively transparent carapace; hence, the heart rate can be easily counted in the intact animal. A rectangular lucite box was constructed to permit regulation of the oxygen tension of the SW flowing over the shrimp. To minimize movement the shrimp was confined within the box by a glass tube whose open ends were covered with pieces of plastic screen. SW was siphoned through this chamber at rate of *ca.* 25 ml/min. The entire system was maintained at 10° C. The experimental animal was placed in the chamber one to two hours before counting commenced. The time for ten heartbeats was measured with the aid of a dissecting microscope. After heart rates were obtained at air-saturation, the oxygen tension was lowered slowly by bubbling nitrogen gas through the SW reservoir. Periodically a micro-Winkler sample was taken from the box and the heart rate was measured immediately thereafter. This procedure was repeated until anoxic conditions were obtained.

Survival time under anoxic conditions

Specimens of *C. californiensis* and *U. pugettensis* were placed in deoxygenated water and maintained until death occurred. Anoxic conditions were obtained by bubbling nitrogen gas through full-strength SW for 1–2 hours. At the end of this time, when shrimp were introduced, only a very small amount of oxygen remained in the water (average 0.011 ml/l). This was considered negligible and was consumed during the experiment, since a micro-Winkler sample at the termination of the experiment yielded essentially zero oxygen. Except for one group experiment (12 shrimp/3.8-liter jar), the shrimp were individually marked and put into jars of anoxic water, which were then sealed tightly and held at 10° C.

Burrow and interstitial water sampling

Water samples from burrows of *Upogebia* were analyzed for dissolved oxygen by the micro-Winkler procedure. Burrows were randomly selected yet checked for signs of recent substrate activity and for the presence of faecal pellets, both of which are indicators of shrimp habitation. To obtain the water samples soft plastic tubing (5 mm diameter) was carefully threaded into the firm burrows (12–20 mm diameter) to a minimum depth of 30 cm. Sample water (10 ml) was drawn up into a glass syringe in such a fashion that no air bubbles were introduced. Large amounts of sand and/or mud were kept from entering the syringe by cover-

ing the end of the sampling tube with cheesecloth. Syringes were sealed with toothpicks, placed on ice and taken directly to the laboratory for analysis.

Water samples from burrows of *Callianassa* were not obtainable because the burrows were collapsible and relatively impermanent. Only interstitial water samples were taken. An interstitial water sampler was constructed of hard, clear, plastic tubing (93 cm long × 1.9 cm diameter) with small holes drilled around the circumference for a distance of 15 cm from the bottom. A solid pointed end enabled the sampler to penetrate 30–60 cm into the substrate. A 10-ml sample of interstitial water was collected and then treated as described above for burrow samples. Sufficient interstitial water samples were not obtainable from the habitats of *Upogebia* because of the exceptionally fine substrate.

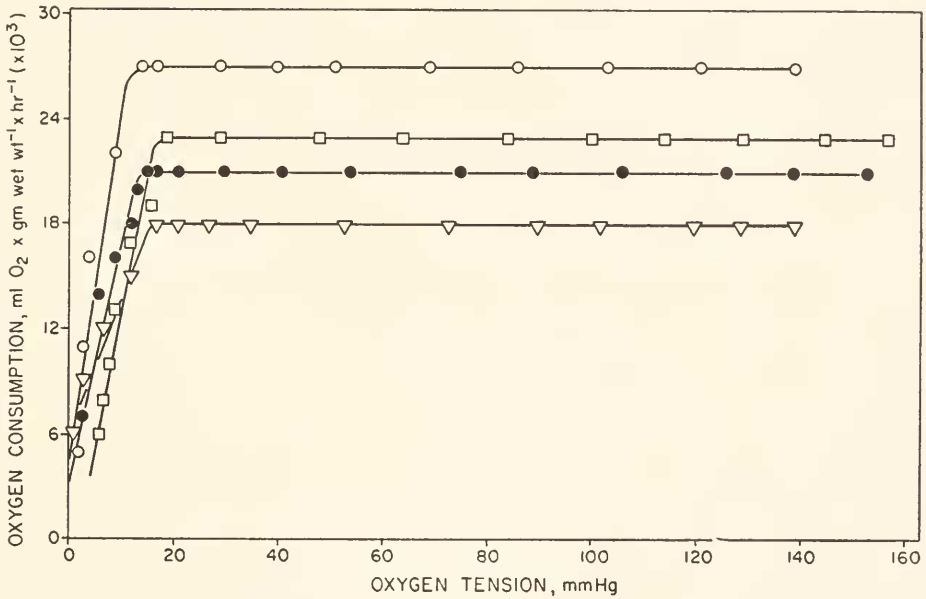

FIGURE 1. Oxygen consumption of *Callianassa californiensis* as a function of oxygen tension at 10° C (○ 7.3 g; □ 8.7 g; ● 5.7 g; ▽ 5.3 g).

RESULTS

Metabolic rate-oxygen tension measurements

The metabolic rates of four individual *Callianassa californiensis* in relation to oxygen tension are seen in Figure 1. Regulation occurs over the range of oxygen tensions from 160 to 20 mm Hg. Datum points are sufficiently different for each individual in this independent range of regulation to warrant separate curves. A distinct break in the metabolic rate curve occurs at 10–20 mm Hg. This range, the oxygen tension at which the metabolic rate ceases to be independent, is called the critical oxygen tension, or T_c (Prosser, 1955). Thus at a T_c of 10–20 mm Hg, corresponding to 0.4–0.8 ml O_2/l or 6.2–12.5% air-saturation, metabolism becomes directly dependent upon external oxygen concentration.

The metabolic rate *vs.* oxygen tension data of four *Upogebia pugettensis* are shown averaged in a curve drawn by inspection (Fig. 2). The metabolic rate is independent of external oxygen concentration as the tension is lowered from air-saturation to approximately 50 mm Hg. Compared to *Callianassa,* the T_c occurs at considerably higher oxygen tensions, 45–50 mm Hg, corresponding to 1.7–1.9 ml O_2/l, or *ca.* 30% air-saturation. No significance is attached to an apparent slight change in slope at approximately 15 mm Hg.

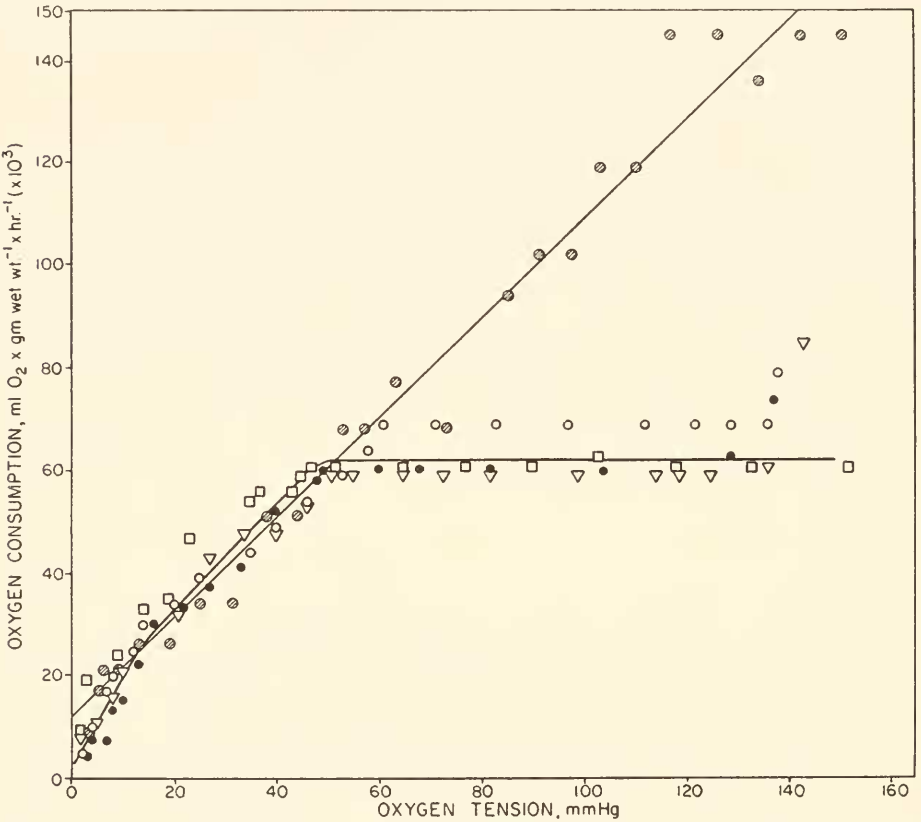

FIGURE 2. Oxygen consumption of non-molted *Upogebia pugettensis* (○ 6.5 g; □ 3.4 g; ● 8.2 g; ▽ 5.9 g) and of a postmolt *U. pugettensis* (shaded circles 3.7 g) as a function of oxygen tension at 10° C.

Metabolic pattern may be altered by experimental conditions. Hiestand (1931) reported that the crayfish *Orconectes* (=*Cambarus*) *virilis* (Hagen), normally a regulator with respect to metabolism, shows a conforming pattern if the jar-animal volume ratio is too small or if the experiment commences at less than air-saturation. In the present experiments consideration is given to this problem by using relatively large jar-to-animal volume ratios.

The metabolic rates of both species were determined at air-saturation. The average metabolic rate for *C. californiensis* ($n = 16$; mean wt 5.3 ±1.5 g) is

0.0291 ± 0.009 ml O_2 ×g wet $wt^{-1} \times hr^{-1}$. *U. pugettensis* ($n = 8$; mean wt 5.7 ± 1.3 g), on the other hand, has a mean metabolic rate of 0.0599 ± 0.014 ml O_2 × g wet $wt^{-1} \times hr^{-1}$, or twice that of *Callianassa.* The difference between the means is significant at the 1% level ($t = |6.67| \geqslant t_{.01} = 2.82$). Effects of activity on oxygen consumption were not measured in the present investigation. We believe that the rates reported above should be considerd as "routine" metabolic rates (as defined by Fry, 1957).

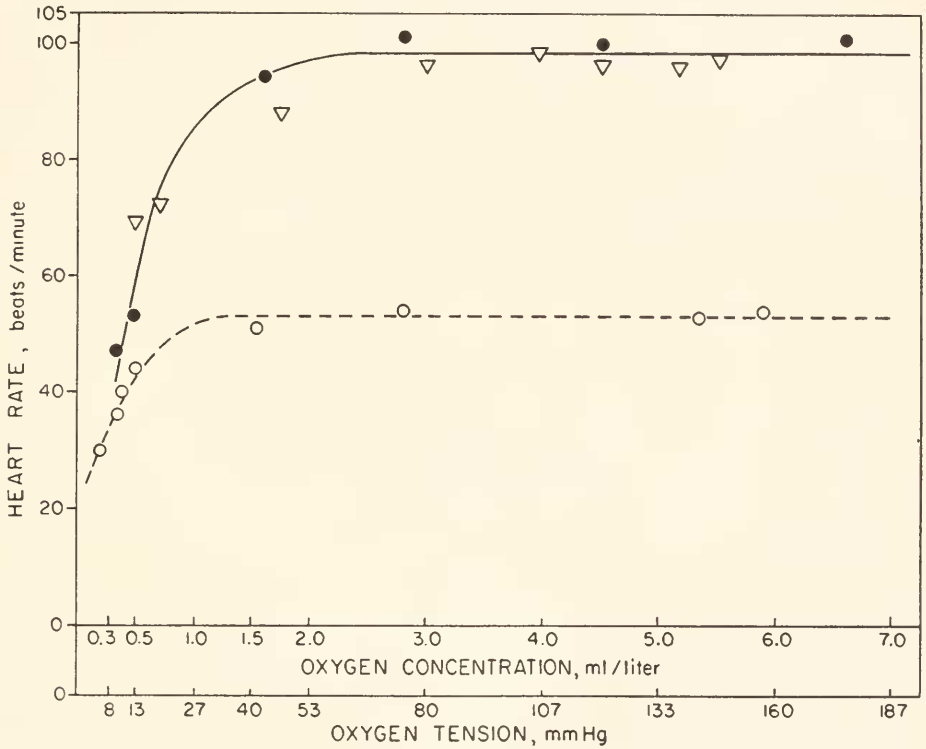

FIGURE 3. Heart rate of *Callianassa californiensis* in beats per minute at various oxygen tensions at 10° C; inactive shrimp ○, ● ; active ▽ ; solid line represents two shrimp.

The metabolic rate curve, determined by liner regression, of a recently molted *U. pugettensis* is also seen in Figure 2. It is apparent that metabolic rate is directly dependent upon external oxygen concentration and that a regulatory phase is absent. This postmolt *Upogebia* has a notably greater respiratory rate at higher oxygen tensions than the non-molted *Upogebia;* however at tensions less than 45–50 mm Hg, metabolic rates are comparable.

A criticism of the sealed jar method used in the present study involves the possible effect of the accumulation of waste products as the animal depletes the available oxygen. However, the fact that shrimp were shown to survive in a sealed jar from three to six days (Table I) leads us to believe that accumulation of waste products in 10–20 hours probably has little effect on the animals.

TABLE I

Survival time in hours for Callianassa californiensis *and* Upogebia pugettensis *individually subjected to anoxic conditions. Averages are presented with the standard deviation*

Animal number	*Callianassa californiensis*			*Upogebia pugettensis*			
	Sex	Wet weight grams	Survival time hours	Animal number	Sex	Wet weight grams	Survival time hours
1	♀	2.8	156	1	♂	1.9	95
2	♂	4.0	111	2	♀	3.7	92
3	♂	4.1	128	3	♂	3.8	72
4	♂	4.3	156	4	♀	5.9	64
5	♂	4.8	108	Average of non-molted animals: 81 ± 15 hours			
6	♂	5.0	187	5	♀	5.5	12
7	♂	5.3	129	6	♂	5.6	42
8	♂	5.6	126	7	♂	7.4	43
9	♂	6.2	132	Average of postmolt animals: 32 ± 18 hours			
10	♂	6.4	179				
11	♂	7.2	110				
Average (all non-molted: 138 ± 27 hours							

Heart rate measurements

The effect of declining oxygen tension upon the heart rate of three *C. californiensis* is illustrated in Figure 3. A single curve for two of the animals has been drawn, while the data for the third animal are shown separately. Activity was operationally defined by movement of legs and pleopods and inactivity by movement of only the gill bailer.

TABLE II

Survival time in hours for non-molted Callianassa californiensis *subjected to anoxic conditions in groups of 12 shrimp per 3.8-liter jar*

Animal number	Group Study A			Group Study B			
	Sex	Wet weight grams	Survival time hours	Animal number	Sex	Wet weight grams	Survival time hours
1	♀	1.5	138	1	♂	2.0	179
2	♀	1.5	138	2	♂	2.1	78
3	♂	1.8	126	3	♀	2.1	129
4	♂	1.9	138	4	♀	2.2	141
5	♂	2.0	126	5	♀	2.3	179
6	♂	2.5	176	6	♀	2.6	129
7	♂	2.7	126	7	♀	3.0	129
8	♂	2.7	126	8	♂	3.2	78
9	♂	2.8	126	9	♂	3.2	78
10	♂	2.8	126	10	♀	3.3	179
11	♂	3.2	176	11	♂	3.4	129
12	♂	3.7	138	12	♂	3.6	78
Average: 138 ± 18 hours				Average: 126 ± 40 hours			

It is seen that heart rates vary considerably between 50 and 100 beats/min and that active and inactive rates overlap. However, it is clear that below *ca.* 1.5 ml O_2/l, the heart rate decreases rapidly with further decrease in tension. The decline in heart rates occurred near the metabolic T_e.

Survival time under anoxic conditions

The survival times for individually tested shrimp are seen in Table I. The average survival time for non-molted *C. californiensis* (138 ± 27hrs) is 1.7 times the average survival time for non-molted *U. pugettensis* (81 ± 15 hrs). However, the average survival time for postmolt *Upogebia* is only 32 ± 18 hrs. The survival times for *Callianassa* tested in groups of 12 (Table II) are essentially identical to those obtained for individually tested shrimp.

The results indicate that survival time under anoxia is independent of both sex and body weight. The possible effect of waste product accumulation and of pH change was not determined. Shrimp were not lethargic under anoxia but appeared to remain active until a few hours before death.

Burrow habitats

U. pugettensis builds relatively permanent burrows in a mud-clay substrate. The burrows were basically U-shaped with side branches, and extended downward to a depth of 2–3 feet. Each burrow had a minimum of two openings which were constricted near the surface and often surrounded by faecal pellets. These observations agree in general with those made by MacGinitie (1930).

On close examination the durable burrow walls, which were smooth and cylindrical in form, were coated with a reddish-brown layer 1–3 mm thick. Microscopic examination of this layer revealed that it is amorphous. In the laboratory the deposit occurred only in containers in which *Upogebia* had burrowed into the mud. Hence, it does not appear to be a function of the substrate alone. Pohl (1946) described a similar dark rust-brown lining (3–7 mm thick) in burrows of *Callianassa major*. Pearse (1945) briefly mentioned that burrows of *Upogebia affiinis* have firm linings like those of *C. major*. The exact nature of the lining and its formation is unknown. We conclude that *Upogebia* inhabits a relatively permanent burrow system with openings at the surface.

The concentration of dissolved oxygen in the water samples obtained from *U. pugettensis* burrows (Table III) at the time of low tide ranged from zero to 0.91 ml/l with an average of 0.58 ml/l. The average depth at which the samples were obtained was 60 cm. The average temperature within the burrows at 30 cm depth was 12.8 ± 1.7° C. Using each burrow water temperature and 33‰, the prevailing salinity of burrow waters throughout the summer, oxygen saturation values were estimated from nomograms (Richards and Corwin, 1956). According to these results burrow water samples were on the average 9.8% of full air-saturation, surface water 70.3% air-saturation, and aerated water in laboratory 97.5% air-saturation.

Burrows of *U. pugettensis* were located at the approximate zero to minus 1 ft tide levels and were thus exposed by the tide for less time than burrows of *C. californiensis* which occurred in higher intertidal areas (zero to +1 ft). Even so,

TABLE III

Amount of dissolved oxygen (ml/l) in water samples obtained from Upogebia pugettensis *burrows located between Coquille Point and Sally's Slough. Data were obtained on three different days at the time of low tide. Averages are given with the standard deviation*

Date	Burrow number	Depth cm	Temp. °C at 30 cm	ml O_2/l	% Air-saturation of burrow water
5/11/66	1a	51	12.0	0.77	12.9
	1b	66	12.0	0.77	12.9
	2	66	12.5	0.88	14.9
	3	66	12.5	0.41	6.9
	4	51	12.0	0.59	9.9
	5	66	12.5	0.88	14.9
5/24/66	6	61	13.0	0.70	12.1
	7	61	12.0	0.75	12.6
	8	61	11.0	0.91	13.5
	9	61	12.5	0.31	5.2
	10	61	11.0	0.62	9.2
	11	61	12.0	0.67	11.2
6/24/66	12	48	—	0.00	00.0
	13	56	16.0	0.39	7.1
	14	61	16.0	0.31	5.6
	15	61	16.2	0.39	7.1
Average		60 ± 6	12.8 ± 1.7	0.58 ± 0.26	9.8 ± 4.1

within one hour after exposure of the burrow openings by the ebbing tide, the oxygen concentration of water in each *Upogebia* burrow decreased by 46–100% (Table IV).

Salient features of *C. californiensis* burrows in the Yaquina Bay region are reported by L. C. Thompson and Pritchard (1969). It is concluded that burrows of *Callianassa* are not firmly constructed, lack a lining, and generally do not have patent openings to the surface during ebb tide.

TABLE IV

Amount of dissolved oxygen (ml/l) in water samples taken from randomly selected Upogebia pugettensis *burrows on May 26, 1966. Each burrow was sampled twice as the tide ebbed. Average sampling depth was 62 ± 3 cm and average temperature was 10.6 ± .4° C*

Burrow number	Burrow diameter cm	Time hours	ml O_2/l	Per cent change
1	1.9	0900	2.70	72
		1000	0.75	
2	1.3	0915	2.18	
		1015	0.00	100
3	1.9	0930	2.44	
		1030	0.99	55
4	2.5	0940	1.56	
		1040	0.83	46
5	1.9	0950	1.14	
		1050	0.36	68

Four interstitial water samples were taken at low tide from the collecting area of *Callianassa* (0.46, 0.58, 0.81 ml O_2/l) and one from the collecting area of *Upogebia* (0.15 ml O_2/l).

Discussion

Callianassa californiensis and *Upogebia pugettensis* at 10° C are metabolic regulators with T_c's far below air-saturation, have low metabolic rates, and are remarkably tolerant to anoxic conditions. Critical oxygen tensions have not been determined for other members of the Thalassinidea. For references on other decapod crustaceans with a T_c below air-saturation see Wolvekamp and Waterman (1960). Mean metabolic rates, within the range of respiratory independence, of *Callianassa* (0.029 ml $O_2 \times$ g wet $wt^{-1} \times hr^{-1}$) and of *Upogebia* (0.059 ml $O_2 \times$ g wet $wt^{-1} \times hr^{-1}$) are comparable to the metabolic rates of other mud-dwelling forms such as the polychaete *Arenicola,* the oligochaete *Enchytraeus* and the echiuroid *Urechis,* 0.031, 0.030, and 0.012 ml $O_2 \times$ g wet $wt^{-1} \times hr^{-1}$, respectively (Prosser and Brown, 1961). Montuori (1913) reported respiration rates of 0.132 and 0.368 ml $O_2 \times$ g wet $wt^{-1} \times hr^{-1}$ at 25° C for *Callianassa subterranea* and *Gebia litoralis,* respectively. Such comparisons, however, have limited significance since experimental conditions in the various investigations differed greatly.

Mudflats have long been recognized as environments impoverished with respect to oxygen (Brafield, 1964; Pearse *et al.,* 1942; ZoBell and Feltham, 1942). Sand or mud substrates greatly impede rapid exchange of oxygen with the overlying waters. Such oxygen as is available is generally restricted to the upper surfaces and to portions of the substrate in contact with overlying oxygenated water via specialized tubes, burrows, *etc.* Tidal exposure may interrupt this exchange altogether. Below the top few centimeters of mud bacteria are largely responsible for anaerobic conditions, hydrogen sulfide, and a highly reducing environment.

In the Yaquina Bay estuary *C. californiensis,* unlike *U. pugettensis,* occupies the higher intertidal levels of the mudflats and is without a permanent burrow system. Burrows of *Callianassa* in the high intertidal area were often uncovered during a low high tide whereas burrows of *Upogebia* were not then exposed. As the tide ebbed, the upper parts of the impermanent sandy burrows tended to collapse and any connection with the overlying oxygen-rich waters was broken. Attempts to trace the burrows and to obtain burrow water samples during ebb tide were unsuccessful. The hypoxic nature of the habitat of *Callianassa* is shown by the interstitial water samples obtained. *Callianassa* does not depend on a water current in its burrow for food but instead sifts the substrate for detritus, burrowing continuously in order to feed (MacGinitie, 1934). Hence, in the absence of a permanent burrow system *Callianassa* is constantly exposed to hypoxic interstitial waters.

The metabolic responses of *C. californiensis* are adaptive to its survival in this hypoxic environment. *Callianassa* is capable of regulating its metabolic rate down to an extremely low T_c. Heart rate appears comparably regulated. Significant bradycardia did not occur until the oxygen tension had dropped below 27 mm Hg. Perhaps the maintenance of a constant heart rate and presumably constant cardiac output enables the shrimp to regulate its metabolic rate as the external medium becomes increasingly hypoxic. Both thalassinids, particularly *Callianassa,* are remarkably resistant to anoxia under laboratory conditions.

A thorough investigation of the mechanisms involved in tolerance of anoxia was beyond the scope of this study. However, several experiments to determine if a compensatory increase in metabolic rate occurred after subjection of shrimps to anoxia were performed. In both *C. californiensis* ($n = 2$) and *U. pugettensis* ($n = 4$) the oxygen consumption following exposure to either 12 or 36 hours of anoxia increased above the pre-anoxic rate. These preliminary experiments suggest that anaerobic metabolism is used by these shrimp during anoxic stress. However, the nature of the anaerobic pathway or pathways, the magnitude of the oxygen debt after longer periods of anoxia, and the metabolic products produced remain to be elucidated. Although von Brand (1946) pointed out that crustaceans, especially decapods, show little tolerance for anoxic conditions, there is more recent evidence for anaerobic metabolism in decapods. Teal and Carey (1967) report an increase in lactate and subsequent decrease in glycogen content in *Uca* under anoxic conditions.

In a recent report Farley and Case (1968) demonstrate "ventilation" behavior by *C. affinis* and *C. californiensis* in response to altered oxygen tension and hypothesize the existence of an oxygen receptor, the direct evidence for which is presently lacking. Comparisons between the species are difficult because of the complex behavioral responses and the lack of comparable experimental conditions for the two species. Thus, under one set of conditions *C. affinis* responded to lowered oxygen and to readmission of oxygenated SW by increasing the stroke frequency of the pleopods and under other conditions *C. californiensis* after experiencing a limited hypoxia migrated toward oxygen-rich SW and increased the stroke frequency of the pleopods.

In the Yaquina Bay estuary water samples from the burrows of *Upogebia* at low tide are markedly hypoxic, becoming more so as the period of tidal exposure increased (Tables III, IV). The data also indicate that during tidal ebb *U. pugettensis* experiences oxygen concentrations well below its T_c; occasionally the oxygen concentration drops to zero. The same may be presumed true for interstitial waters of mud, although the data are more limited. In the present study the mean concentration of oxygen in burrow waters of *Upogebia* is 0.58 ml O_2/l. Only one reliable interstitial water sample from the *Upogebia* collecting area could be obtained with the sampling device described (0.15 ml O_2/l).

Upogebia shows physiological and ecological adaptations to these hypoxic conditions. Its metabolic rate is among the lowest reported for Crustacea (Wolvekamp and Waterman, 1960). Non-molted shrimp regulate metabolism above 45–50 mm Hg and can tolerate more than two days without oxygen, which at the zero tide level far exceeds the maximum tidal exposure of Pacific coast mudflats (MacGinitie, 1935). The permanent burrow system and its apertures represent open channels for exchange with the oxygen-rich overlying waters. More important, *Upogebia* actively irrigates its burrows, and as a suspension feeder, is dependent upon such irrigation (Jørgensen, 1966; MacGinitie, 1930). As a consequence *Upogebia* probably experiences in its burrows higher oxygen concentrations than those of neighboring interstitial waters, as is true for other tube-dwellers in hypoxic habitats. For instance, the burrow waters of the polychaete *Arenicola* have an oxygen concentration (0.50 ml O_2/l), twice that of nearby interstitial waters (Jones, 1955). The tube material of a sedentary polychaete, *Mesochaetopterus taylori,* apparently acts as a protective diffusion barrier to oxygen, hence the tube waters

contain significantly more oxygen than do the surrounding anoxic interstitial waters (Petersen and Johansen, 1967).

Information about the effect of molting on the respiration of crustaceans is limited but it is generally agreed that respiration increases at the time of ecdysis (Passano, 1960). The present data suggest that postmolt *Upogebia* are relatively more oxygen-dependent and less resistant to anoxia than are non-molted animals. Nothing is known about the behavior of *Upogebia* during molting under natural environmental conditions.

Metabolic requirements, indicators of which are T_c, metabolic rate, and tolerance to anoxia, generally reflect oxygen availability in the environment. Animals inhabiting environments high in oxygen usually have greater metabolic requirements than those inhabiting environments low in oxygen. Isopods, ephemerid nymphs and trichopterid larvae from ponds have lower metabolic rates, survive longer in low oxygen and have lower T_c's than the same or related species from swift streams (Fox and Simmonds, 1933; Fox, Wingfield and Simmonds, 1937). Walshe (1948), emphasizing that differences in metabolic requirements reflect oxygen availability in the habitat, reported that stream chironomid larvae (metabolic conformers) have higher metabolic rates and are less resistant to hypoxia than those from ditches (metabolic regulators). Bovbjerg (1952) found that *Cambarus fodiens,* a mud-burrowing crayfish of ponds, survived anoxic conditions four times longer than *C. propinquus,* an inhabitant of swift streams.

In conclusion, emphasis is placed on the adaptive significance of the respiratory responses reported for mud-dwelling thalassinids in the present study. *C. californiensis* and *U. pugettensis* live in mudflats, an environment relatively low in oxygen. Both show the following physiological mechanisms: (1) low metabolic rates; (2) metabolic regulation with a T_c below 50 mm Hg; and (3) survival in anoxia for at least three days. These mechanisms correlate well with a hypoxic habitat and are therefore considered adaptive. Closer analysis reveals quantitative differences in their respiratory responses. *Upogebia* has a greater metabolic rate, higher T_c, and is less able to tolerate anoxia than *Callianassa.* Despite the paradoxical situation of living in a substrate poorer in oxygen, *Upogebia* probably has in fact more oxygen available in its specific niche within the mudflat habitat than does *Callianassa;* hence, metabolic requirements of *U. pugettensis* are greater and regulatory features are less pronounced than in *C. californiensis.* The present study supports the generality that metabolic requirements and the availability of oxygen in the environment are closely correlated.

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Summary

1. The respiratory responses of two mud-shrimps, *Callianassa californiensis* and *Upogebia pugettensis* (Thalassinidea), from Yaquina Bay, Newport, Oregon, were measured.

2. Both species are metabolic regulators, showing oxygen-independent respiration above the critical oxygen tension for *C. californiensis* of 10–20 mm Hg (6.–12.5% air-saturation) and for *U. pugettensis* of 45–50 mm Hg (28–31% air-saturation).

3. Within the independent range of respiration, *C. californiensis* has a mean metabolic rate of 0.029 ml $O_2 \times$g wet wt$^{-1} \times$ hr^{-1}, which is significantly lower than that of *U. pugettensis* (0.059 ml $O_2 \times$ g wet wt$^{-1} \times$ hr^{-1}).

4. Heart rates of *C. californiensis* subjected to diminishing oxygen tensions show a regulatory pattern similar to the metabolic rate, with bradycardia occurring at *ca.* 27 mm Hg.

5. Both species are tolerant to anoxia. *C. californiensis* survives approximately 5.7 days and *U. pugettensis* 3.3 days under such conditions.

6. Preliminary data suggest that postmolt *U. pugettensis* do not regulate and therefore are oxygen-dependent throughout the range tested.

7. The mean concentration of oxygen in water obtained from exposed *U. pugettensis* burrows is 0.58 ml O_2/l, well above that of interstitial water.

8. *C. californiensis,* in contrast to *U. pugettensis,* does not construct firm burrows and is probably directly exposed to hypoxic interstitial waters.

9. Both species have respiratory adaptations for survival in a hypoxic environment. Quantitative differences in the metabolic requirements of the two species reflect the availability of oxygen in their respective niches within the mudflat biotope.

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